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Research Article

Evaluating spatially explicit management alternatives for an invasive species in a riverine network

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Abstract

Invasive species have substantial ecological and economic costs and removing them can require large investments by management agencies. Optimal spatial allocation of removal effort is critical for efficient and effective management of invasive species. Using a series of ecologically informed model simulations, we evaluated and compared different spatially explicit removal strategies for invasive rusty crayfish (*Faxonius rusticus*) in the John Day River, USA. We assessed strategies in terms of their performance on three likely management objectives: suppression (minimise overall population abundance), containment (minimise the spatial extent of invasion) and prevention (minimise spread into a specific area). We developed five spatial removal strategies to achieve those objectives, denoted as: Target Abundance (removal at locations with the highest population abundance), Target Growth (removal at locations with the highest population growth), Target Edges (removal at the most distant locations in the river), Target Downstream (removal at the most downstream invaded segments on the Mainstem), and Target Random (removal at randomly selected locations). Each strategy was assessed at various effort levels, referring to the number of spatial segments in the river in which removals were conducted, after seven years of management. We identified the alternative that best achieved each objective, based on decision criteria for risk-neutral and risk-averse decision-makers and further evaluated strategies based on Pareto efficiency, which identifies the set of alternatives for which an improvement on one objective cannot be had without a decline in performance on another. We found that Target Abundance and Target Growth strategies best achieved the suppression objective, for risk neutral and risk averse decision-makers, respectively and Target Downstream was always best in achieving the prevention objective across both types of decision-makers. No single strategy consistently performed best in terms of the containment objective. In terms of all three objectives, Target Downstream was consistently Pareto efficient across all levels of management effort and both decision criteria. The modelling framework we provided is adaptable to a variety of riverine invasive species to help assess and compare spatial management strategies.

Key words: Aquatic invasive species, crayfish, invasive species management, spatially explicit model

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Introduction

Invasive species are a primary threat to global biodiversity, economies and human health (Pyšek and Richardson 2010; Early et al. 2016; Diagne et al. 2021). Managers of invasive species often seek to reduce two of the main contributors to negative species impacts: population abundance and range extent (Parker et al. 1999; Kumschick et al. 2015). However, desired management outcomes can be challenging to achieve due to imperfect detection, the ineffectiveness of available management actions and invasive species whose rapid growth and spread can largely nullify the effect of management (Rendall et al. 2021; Cuthbert et al. 2022). In addition, with widespread invasions and constrained budgets, natural resource managers are frequently limited by when and where they can manage (Donlan et al. 2015; Wenger et al. 2018). Approaches for identifying effective spatiotemporal allocation of management effort remains a primary need of managers.

Predicting the effectiveness of alternative spatial allocations of management effort is challenging, yet choosing the most effective allocation is critical for successful population suppression or containment of abundant invaders (Travis and Park 2004; Eppinga et al. 2021). Various alternative spatial allocation rules of thumb have been posited for invasive species management to achieve objectives of suppressing and limiting the spread of invasive species. For example, to suppress population size, the "targeting the source" rule involves allocating management effort in locations where the invasive population is the most abundant (Baker 2017) and to limit invasive species spread, the "managing the edges" rule involves expending effort at the invasion front (Bradley 1988; Moody and Mack 1988; Bossard et al. 2000). Ultimately, however, in any given case, the optimal spatial allocation of effort will depend on management objectives, the ecology of the invader and the characteristics of the invaded system. For instance, if dispersal of the invasive species is small relative to population growth, removal at the edges of the invasion may be a more successful approach in reducing spread of an invader because efforts to remove at the core of the population may be overwhelmed by population growth (Baker 2017).

Quantitative population models are useful tools for evaluating invasive species management strategies in a virtual environment before management is implemented (García-Díaz et al. 2019; Thompson et al. 2021; Hudina et al. 2022). Simulation models can be efficiently used to compare a variety of alternatives under varying ecological and management assumptions without the substantial time and expense of on-the-ground experiments. In particular, spatially explicit population models are powerful tools for modelling population growth and spread and evaluating alternative spatial allocations of management effort (Epanchin-Niell and Hastings 2010; Bertolino et al. 2020; Goodenberger et al. 2020). Spatially explicit population models are especially useful in largescale invasion contexts to identify crucial locations wherein management resources could be directed to reduce further expansion and growth of the invasive population (Pepin et al. 2019).

A number of spatially explicit population models have been developed to evaluate spatial allocation of management effort in terrestrial invasion contexts (e.g. Epanchin-Niell et al. (2012); Baker and Bode (2016); Pepin et al. (2020)); however, such models have rarely been developed for freshwater contexts (but see Albers et al. (2018) and Kallis et al. (2023)). Spatially explicit population models in rivers

are particularly difficult to parameterise due to challenges imposed by dendritic networks, including understanding individual movements (Corrales et al. 2020; Caradima et al. 2021). For instance, it is rare to observe marked individuals in aquatic systems (Ogburn et al. 2017), limiting the utility of tools such as multi-state mark-recapture models (Arnason 1973) for understanding movement. In addition, software for mechanistic modelling of animal movement has primarily been developed for terrestrial systems and only recently has been advanced for modelling animal movements in rivers (Quaglietta and Porto 2019). However, as technology for studying movement continues to develop for aquatic species, spatially explicit population models may be increasingly valuable tools for informing management in river systems.

In this study, we used a spatially explicit population model to assess removal alternatives for the management of invasive rusty crayfish (*Faxonius rusticus*) in the John Day River (JDR) of Oregon, USA, a major tributary of the Columbia River. The JDR is one of the largest free-flowing rivers in the United States and holds high conservation importance as it supports a variety of salmon species of significant cultural and economic value, such as endangered spring Chinook salmon (*Oncorhynchus tshawytscha*) and the threatened steelhead (*Oncorhynchus mykiss*). The presence of rusty crayfish in the JDR remains a significant concern because they are spreading rapidly (18 km year^{-1}), reaching high local abundances (up to 50 m^{-2}) and have the potential to inflict severe ecological impacts due to polytrophic and generalist feeding habits (Olden et al. 2011; Twardochleb et al. 2013).

Using a spatially explicit population model for rusty crayfish, we assessed alternative management strategies involving different spatial allocations of removal effort over a multi-year management time horizon. We evaluated the alternatives, based on performance of three management objectives that capture commonly held values of natural resource managers concerned with invasive species: suppression (minimise the overall population abundance), containment (minimise the spatial extent of invasion) and prevention (minimise spread into a particular area). The results from this study broadly seek to provide a template for the evaluation of invasive species management strategies in dendritic riverine systems.

Methods

Study system and management context

Rusty crayfish are regarded as a highly-invasive species, particularly in the JDR, due to high population growth and generalist feeding habits. Rusty crayfish have been implicated in the decline of macrophytes, aquatic insects, snails and fishes across the introduced range (Twardochleb et al. 2013). We simulated alternative strategies for managing rusty crayfish in a portion of the JDR where the species is anticipated to negatively impact the ecosystem (Falke et al. 2013; McHugh et al. 2017; Fig. 1). We divided this portion of the JDR into 35 segments of 20-km length, the maximum possible size of a 'management unit' wherein removal could be conducted, henceforth termed segments. The locations where crayfish management occurred corresponded to specific segments, selected annually (Fig. 1, Suppl. material 1: fig. S5).

Figure 1. Map of the John Day River (JDR) Basin and tributaries (Mainstem, North Fork, Middle Fork, South Fork and Murderers Creek). The dark blue region of the JDR represents the spatial extent of this study (35 segments). The light blue regions of the JDR Basin are not included in our simulations. The JDR flows into the Columbia River.

A range of management objectives are of interest to invasive species managers, including – broadly – eradication, suppression (i.e. minimising total abundance), containment (i.e. minimising range size or total spatial extent) and prevention (i.e. minimising spread into a particular geographic location, for example, the Columbia River for this study) (Gherardi et al. 2011; Rytwinski et al. 2019). Here, we focused on the latter three – suppression, containment and prevention – as eradication does not appear to be achievable, based on our results and other studies (Messager and Olden 2018).

We developed management strategies with suppression, containment, and prevention in mind (Table 1). We developed a strategy called Target Abundance primarily to address the suppression objective, with removal effort in segments with the highest total crayfish abundance. We also developed the Target Growth strategy primarily to address the suppression objective, with removal effort in segments with the highest population growth. We created the Target Edges strategy to address the containment objective, with removal effort at the invasion edges with the highest abundance and at segments adjacent to invasion edges depending on the number of segments receiving removal effort, again prioritised by abundance. An invasion edge refers to the most upstream invaded segment on the Mainstem, North Fork, Middle Fork, South Fork and Murderers Creek and the most downstream invaded segment on the Mainstem (Fig. 1). We developed the strategy Target Downstream to address both the prevention and containment objectives, with removal effort at the most downstream segments on the Mainstem with crayfish present. We also evaluated a Target Random strategy, with removal at randomly selected segments,

Table 1. Twenty-one management alternatives that were simulated for removal of rusty crayfish in the John Day River System, including the broad management strategy, the number of segments (and percentage of the modelled system) receiving removal effort and the specific objectives targeted by the management strategy: suppression (i.e. minimise total abundance), containment (i.e. minimise total spatial extent) and prevention (i.e. minimise spread into the Columbia River). Removals were simulated to occur June through September for ten trap-nights per month. Segments receiving removal effort were selected annually given the alternative and the simulated system state.

Management Strategy	No. Segments Receiving Removal Effort (% of the JDR managed)	Objective(s) Targeted
No removals	0 (0%)	None
Target Abundance: remove at segments with highest total crayfish abundance	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Suppression
Target Growth: remove at segments with highest crayfish population growth	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Suppression
Target Edges: remove at edges of invasion with the highest abundance (i.e. invaded segments most downstream on the Mainstem and most upstream on the Mainstem, North Fork, Middle Fork, South Fork or Murderers Creek)	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Containment
Target Downstream: remove at the most downstream segments on the Mainstem with crayfish abundance	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Containment/ Prevention
Target Random: remove at randomly selected segments	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Suppression/ Containment/ Prevention

with a new random selection each year. Given random selection under this strategy, segments with no crayfish could be selected for management. Finally, we evaluated a No Removals strategy to represent the status quo in the JDR.

For each of the broad management strategies (except No Removals), we simulated various levels of removal effort, which corresponded to the number of segments where removal was simulated (Table 1). We assumed removal of crayfish via trapping and physical removal, which is the most common method for crayfish (Freeman et al. 2010; Gherardi et al. 2011; Manfrin et al. 2019). We tested four levels of removal effort, such that removal was simulated at 1, 4, 8 or 16 segments out of the total 35 segments, representing approximately 3%, 11%, 23% or 45% of the modelled system (capped at the maximum feasible spatial coverage for management). Thus, with five broad removal strategies, each with four levels of effort, plus the No Removals strategy, we evaluated 21 total management alternatives. The segments selected for removal remained fixed during a year and were identified annually according to the management strategy. In addition, given high-flow conditions during the autumn and winter months that limit accessibility, we simulated removals only during June through September, with removals occurring over ten trap-nights in each of those months. We evaluated management strategies over a seven-year management time horizon.

Model structure

We developed a spatially explicit population model to simulate rusty crayfish removal, growth and movement. Our simulation model largely follows the ecological process described by Link et al. (2018) in their model for estimating abundance, growth, movement and detection efficiency using spatially referenced counts of removals from an invasive population; the primary difference is our addition of age structure. In our model, we track abundance of the population by spatial unit (i.e. a river segment) and allow the population to grow and move and to be removed as a function of removal effort. We assumed that removals occurred on ten consecutive trap-nights each month, during the months of June through September

each year and that all population growth and movement occurred between each monthly removal period. The time step in the simulation model is primarily a monthly time step, but switches to a daily time step during periods of removal, when the population is otherwise closed.

Messager and Olden (2018) previously simulated the spread and removal of rusty crayfish in the JDR with a spatially explicit individual-based model. We drew many parameter values from that study, as well as the literature (see Appendix 1 for detailed parameter value descriptions). In our model, segments of 20-km length were indexed by $i = 1, 2,. . ., I$ ($I = 35$ segments), months were indexed by $j = 1, 2, . . . J$ ($J = 84$ months) and trap-nights within months were indexed by $k = 1, …, K$ ($K = 10$ trap-nights). Only females were modelled and age class was indexed by $a = 0, 1, 2$ and 3 (where 0 = 0–1 year olds, 1 = 1–2 year olds, 2 = 2–3 year olds and 3 = older than 3). In the following sections, we describe the specific modelling structures for the removal, population growth and movement sub-models.

Removal sub-model

The removal sub-model allowed for simulation of trapping and removal of crayfish. We defined $N_{i,j,k,a}$ as the abundance at segment i before the k^{th} trap night during month j, for age a and $Y_{i,j,k,a}$ as the number of crayfish removed. We assumed age-0 individuals were too small to be removed by typical trapping methods (Ogle and Kret 2008). Hence, crayfish abundance and removals for age classes $a = 1, 2, 3$ and for trap nights $k = 2,…, K$ were:

$$N_{i,j,k,a} = N_{i,j,(k\text{-}1),a} - Y_{i,j,(k\text{-}1),a} \tag{1}$$

$$Y_{i,j,k,a} \sim \text{Binomial}(N_{i,j,k,a}, p) \tag{2}$$

with effective removal probability, p, modelled as:

$$p = 0.25\theta \tag{3}$$

where 0.25 indicates that a fixed 25% of the segment was covered with traps, which represents a reasonable maximum spatial coverage. We expressed θ as the probability of capture for a crayfish within the trappable area around a single trap. No information was available with which to estimate θ, so we defined a Uniform (0.1, 0.5) distribution to represent our uncertain judgment about this parameter.

The calculation of $N_{i,j,k,a}$, for $j > 1$ and $k = 1$, i.e. abundance on the first trap-night in all removal months after the first month, is described further in the movement sub-model section and initial population $N_{i,j,k,a}$ for $j = 1$ and $k = 1$ is described in the simulation study implementation section.

Population growth sub-model

After $K = 10$ trap nights, we calculated $R_{i,j,a}$, the population remaining after removal as:

$$R_{i,j,a} = N_{i,j,K,a} - Y_{i,j,K,a} \tag{4}$$

We then initiated the population growth sub-model based on $R_{i,j,a}$. Since the model was age-structured, we calculated $D_{i,j,a}$, defined as the number in the population after population growth. $D_{i,j,a}$ was based on a time-varying Leslie matrix, L_j, containing survival probabilities and fecundity rates for each age class. Since survival was applied monthly, while age transitions and reproduction occurred yearly, we created two Leslie matrices, one for all months excluding June and one for June, when age transitions and reproduction occurred. For months excluding June, L_j was:

$$\begin{pmatrix} \varphi_0 & 0 & 0 & 0 \\ 0 & \varphi_1 & 0 & 0 \\ 0 & 0 & \varphi_2 & 0 \\ 0 & 0 & 0 & \varphi_3 \end{pmatrix} \tag{5}$$

where φ_a were monthly survival rates for each age class (i.e. in months excluding June, population "growth" was strictly negative). In June, the population underwent age transition and reproduction and the post-breeding census matrix was:

$$\begin{pmatrix} \varphi_0 f_1 m_1 & \varphi_1 f_2 m_2 & \varphi_2 f_3 m_3 & \varphi_3 f_3 m_3 \\ \varphi_0 & 0 & 0 & 0 \\ 0 & \varphi_1 & 0 & 0 \\ 0 & 0 & \varphi_2 & \varphi_3 \end{pmatrix} \tag{6}$$

where f_a represented age class-specific fecundity rates and m_a represented the fraction of mature females out of total females in each age class, for a = 1, 2 and 3 (Messager and Olden 2018). The first row provides each age class' contribution to the age-0 crayfish entering the population on 1 June.

We sampled rates φ_a, f_a and m_a from normal distributions. Survival rate φ_a had mean values of 0.81, 0.97, 0.94 and 0.72 with a standard deviation of 0.1 for a = 0, 1, 2 and 3, respectively and bounded between 0 and 1 (Suppl. material 1: table S3; Messager and Olden 2018). The fecundity rates, f_a, had mean values of 80, 120 and 150 with standard deviations of 10, 20 and 40 for a = 1, 2 and 3, respectively and bounded between 0 and ∞ (Suppl. material 1: fig S3; Messager and Olden 2018). The fraction of mature females, m_a, had mean values of 0.1, 0.8 and 0.9 for a = 1, 2 and 3, respectively, with a standard deviation of 0.1 and bounded between 0 and 1 (Suppl. material 1: table S3; Messager and Olden 2018). $D_{i,j,a}$ was calculated as:

$$D_{i,j,a} = L_j \times R_{i,j,a} \tag{7}$$

and rounded upwards.

We assumed that the number of crayfish in each segment could at most be 12,166,668, which was calculated as twice the maximum density (30.4 crayfish/m^2) observed in a 2016 field study for a population assumed to be at the stable age structure (Messager and Olden 2018). If the number of crayfish in a segment was greater than the carrying capacity, the excess number of crayfish was first subtracted from age class 0 individuals, $D_{i,j,0}$, since that age class would likely be the most negatively impacted by density-dependent processes. Any remaining crayfish were subtracted from the other age classes, in order of increasing age.

Movement sub-model

After population growth, we modelled the monthly movement of crayfish between adjacent segments. We first calculated the number of crayfish that remained in each segment. The probability of staying in each segment was:

$$m_{\text{stay}} = 1 - 0.5\pi(1 - \mathrm{u}_{i,j}) \tag{8}$$

In this expression, 0.5 indicates that only one half of the crayfish population in any segment was available to move because the size of a single segment was 20 km and crayfish do not disperse more than 5 km in a single month (Messager and Olden 2018). The parameter π is the probability of moving, which ranged between 0.05 and 0.25 by increments of 0.05 (Messager and Olden 2018, Suppl. material 1: table S3). Next, $\mathrm{u}_{i,j}$ represents the proportion of crayfish that stayed in a current segment due to temperature constraints. To calculate this proportion, we obtained segment-level temperature data and calculated the fraction of days each month in which temperature was less than 6 °C, such that crayfish movement is physiologically unfeasible (Hamr 1997; Messager and Olden 2018). Hence, the term 1- $\mathrm{u}_{i,j}$ represented the probability that crayfish were not restricted in their movement by temperature constraints. Then, for a = 1, 2 and 3, the number of crayfish that stayed in a segment was calculated as:

$$D_{i,j,a}^{\text{stay}} \sim \text{Binomial}\left(D_{i,j,a}, m_{\text{stay}}\right) \tag{9}$$

Next, we calculated crayfish that moved downstream:

$$D_{i,j,a}^{\text{down}} \sim \text{Binomial}\left(D_{i,j,a} - D_{i,j,a}^{\text{stay}}, m_{\text{down}}\right) \tag{10}$$

where $D_{i,j,a} - D_{i,j,a}^{\text{stay}}$ was the number of crayfish that did not stay in segment j and the probability of moving downstream conditional on moving was m_{down}, which was drawn from Uniform(0.5, 1) (Messager and Olden 2018). Then, for segments not adjacent to a river fork, we calculated the number of individuals moving upstream as:

$$D_{i,j,a}^{\text{up}} = D_{i,j,a} - D_{i,j,a}^{\text{stay}} - D_{i,j,a}^{\text{down}} \tag{11}$$

Crayfish in some segments could move upstream within the same tributary and move upstream to a new fork (i.e. segments 6, 8, 25 and 31, Suppl. material 1: fig. S5) and we needed to implement a bifurcation movement process. Due to the hydrology of the JDR, we only needed to incorporate the bifurcation process in upstream movement. In these few segments, we assumed upstream movement within the same fork and to a different fork had equal probability. Therefore, in those segments, we calculated the number of individuals that moved upstream as:

$$D_{i,j,a}^{\text{up}} = \frac{D_{i,j,a} - D_{i,j,a}^{\text{stay}} - D_{i,j,a}^{\text{down}}}{2} \tag{12}$$

rounded downwards and the number of crayfish that moved to a new fork as:

$$D_{i,j,a}^{\text{fork}} = D_{i,j,a} - D_{i,j,a}^{\text{stay}} - D_{i,j,a}^{\text{down}} - D_{i,j,a}^{\text{up}} \tag{13}$$

Finally, we redistributed crayfish in the river according to their recent movement. However, for a = 0, $D_{i,j,a} = N^{\text{redistribute}}_{i,j,a}$, since we assumed that age-0 individuals do not move (Messager and Olden 2018). Hence, we calculated the redistributed population as:

$$N^{\text{redistribute}}_{i,j,a} = D^{\text{stay}}_{i,j,a} + \sum_{h \in \text{down}_i} D^{\text{down}}_{h,j,a} + D^{\text{up}}_{up_i,j,a} + D^{\text{fork}}_{fork_i,j,a} \tag{14}$$

where the first term represented the population that stayed in segment i. The second term is the population that moved downstream into i from segments $h \in \text{down}_i$, where down_i was the set of segments from which crayfish could move downstream to i. The third term represents the number of crayfish that moved into i from upstream segment up_i. Finally, the fourth term is the number of crayfish that moved upstream into i from a segment in a different fork, fork_i (see Suppl. material 1: fig. S5 for a graphical representation of each river segment in the JDR and downstream movement directions). We assumed that, in the most upstream segments in all forks, no crayfish could move upstream out of that fork. We also assumed that crayfish in the most downstream segment in the Mainstem could move out of the JDR, which allowed us to calculate the number of crayfish that entered the Columbia River.

Once we completed the movement process, we calculated abundance at the beginning of the next month j + 1 as $N_{i,(j+1),1,a} = N^{\text{redistribute}}_{i,j,a}$. For the months June, July, August and September, removal, population growth and movement occurred and, for all other months, only population growth and movement occurred. At the end of May, before June crayfish removal, the abundance of total crayfish in a = 1, 2 and 3 (i.e. excluding a = 0) at each segment was assessed and the locations where removal would occur that June through September were informed by the simulated management strategy.

Simulation study implementation

Population simulations were coded in R (R version 4.3.1, R Core Team 2023). We simulated each of the 21 management alternatives under the same 20 parameter sets to account for parametric uncertainty for each parameter (e.g. survival, fecundity and movement rates) and ran 50 simulations for each parameter set to account for stochasticity. To create the parameter sets, we performed 20 independent draws from the parametric distributions provided in the model descriptions (Suppl. material 1: table S3).

Each simulation under each alternative was initialised with the same segment-level population, which was informed by an intensive crayfish survey in 2016 (Suppl. material 1: fig. S1, Messager and Olden 2018). Since rusty crayfish were likely introduced to the JDR in 1999, we assumed that, by 2016, the population had reached a stable age distribution and for each parameter set we calculated an annual Leslie matrix and then calculated the stable age distribution as the eigenvector associated with the largest eigenvalue of the annual Leslie matrix:

$$\begin{pmatrix} \varphi_0^{12} f_1 m_1 & \varphi_1^{12} f_2 m_2 & \varphi_2^{12} f_3 m_3 & \varphi_3^{12} f_3 m_3 \\ \varphi_0^{12} & 0 & 0 & 0 \\ 0 & \varphi_1^{12} & 0 & 0 \\ 0 & 0 & \varphi_2^{12} & \varphi_3^{12} \end{pmatrix} \tag{15}$$

Therefore, although the segment-level population was the same across parameter sets, the distribution of each age class at each segment differed between parameter sets.

Evaluation of alternatives

We evaluated the performance on each objective – suppression, containment and prevention – under each alternative. We only considered adults (a = 1, 2 and 3) in our calculation of management outcomes because of the demonstrated ecological effects of adult crayfish. We expressed management outcomes for the suppression objective for each simulation as the total crayfish population size after 7 years of management (month J = 84), $\sum_{i=1}^{I}\sum_{a=1}^{A} N_{i,J,a}^{\text{redistribute}}$ (with the objective of minimising this quantity); the number of years since the last extensive survey of rusty crayfish in the JDR. We expressed management outcomes under the containment objective for each simulation as the proportion of segments in which rusty crayfish abundance exceeded a threshold after 7 years of management (with the objective of minimising this quantity). We defined this threshold as 10% of the average abundance for a = 1, 2 and 3 under the No Removals strategy and assumed that a segment-specific abundance below this threshold would represent functional eradication (sensu Green and Grosholz (2021)) in this system and values above this threshold would indicate the segment had an ecologically impactful crayfish population. We expressed management outcomes under the prevention objective for each simulation as the cumulative number of crayfish that moved out of the JDR and entered the Columbia River (with the objective of minimising this quantity). This was calculated as $\sum_{j=1}^{J}\sum_{a=1}^{A} D_{i,J,a}^{\text{down}}$ for the most downstream segment i in the Mainstem of the JDR (i = 22, Suppl. material 1: fig. S5).

We considered two decision criteria: expected value and mini-max. The expected value criterion, used for risk-neutral decision-makers, selects for the management alternative with the best expected performance (i.e. average simulated value) over simulations. The mini-max criterion is a risk-averse decision criterion that selects for the alternative that minimises the maximum possible loss given uncertainty (i.e. the worst outcome over all simulations) (Savage 1951).

Multiple objective assessment

Multiple objective decisions are common in natural resources management (Converse 2020) and we were interested in evaluating strategies across our three objectives simultaneously. Pareto-efficient alternatives, or non-dominated alternatives, are the alternatives within a set under which the outcome on one objective cannot be improved without a reduction in another objective (Cohon 1978; Kennedy et al. 2008). Non-optimal alternatives, or dominated alternatives, are clearly inferior because some other alternative in the set performs at least as well as the dominated alternative on all objectives and performs strictly better on at least one. We found the Pareto front, the set of Pareto-efficient alternatives, using both the expected value and mini-max criteria, across our three objectives: suppression, containment and prevention. This is the set of alternatives that strikes some efficient trade-off between suppressing the population, containing it and preventing it from entering the Columbia River.

Results

The Target Abundance strategy performed best on the suppression objective with respect to expected value, regardless of the number of segments receiving removal effort (Fig. 2A, Table 2). The final population distribution further revealed that this strategy led to overall population suppression in the JDR (Fig. 3; with 16 segments of removal effort; see Suppl. material 1: fig. S2 for other segments receiving removal effort). However, this strategy was not optimal under the risk-averse mini-max criterion for the suppression objective (Table 3). In addition, the Target Abundance performed poorly on the containment and prevention objectives across all levels of removal effort (Tables 2, 3).

The Target Growth strategy, across all levels of removal effort, performed best on the mini-max criterion for the suppression objective (Table 3), yet was the worst in terms of expected value (Table 2, Fig. 2A). Target Growth had the best expected value performance for the containment objective given one segment of removal effort and was the second-best strategy for this objective given 4, 8 or 16 segments of effort (Table 2). This strategy was never optimal with respect to the prevention objective given either the expected value or the mini-max criteria and any level of removal effort (Tables 2, 3).

The Target Edges strategy performed poorly on the suppression objective across all levels of removal effort (Tables 2, 3). However, with 16 segments of effort, this strategy did suppress crayfish population at the "edges" of invasion, as there were low final populations in all major tributaries of the JDR and in the most upstream and downstream segments of the Mainstem of the JDR (Fig. 3). Therefore, this strategy had the best expected value for the containment objective for 16 segments of effort (Table 2, Fig. 2B).

Target Downstream was the best strategy on the prevention objective regardless of the decision criterion and regardless of the number of segments of removal effort (Tables 2, 3, Figs 2C, 3). In addition, this strategy performed the best in terms of expected value for the containment objective for 4 or 8 segments of effort (Table 2). Overall, the Target Downstream strategy did not perform well on the suppression objective (Tables 2, 3).

The Target Random strategy, in terms of the mini-max criterion, was the worst strategy for both suppression and prevention objectives and performed equally as bad as all other strategies on the containment objective, across all numbers of segments receiving removal effort (Table 3). Compared to other strategies, Target Random was neither the optimal nor the worst strategy in terms of the expected value criterion across all objectives. Overall, the Target Random strategy had variable outcomes on all objectives, as shown by the various outlier values (Fig. 2). However, Target Random did perform better than No removals. Overall, the No removals strategy performed the worst across every objective and criterion (Tables 2, 3).

The Pareto efficient strategies, in terms of expected value, included Target Abundance, Target Downstream and Target Random across all levels of removal effort (Table 2). For 4 and 8 segments of effort, the dominated strategies (Target Growth and Target Edges) were dominated by the Target Downstream strategy and, for 16 segments of effort, the dominated strategy (Target Growth) was dominated by Target Edges (Table 2). In terms of the mini-max criterion, Target Growth and Target Downstream were Pareto efficient regardless of the level of removal effort (Table 3). For 4, 8 and 16 segments of effort, the Target Random strategy was dominated by every other strategy (Table 3).

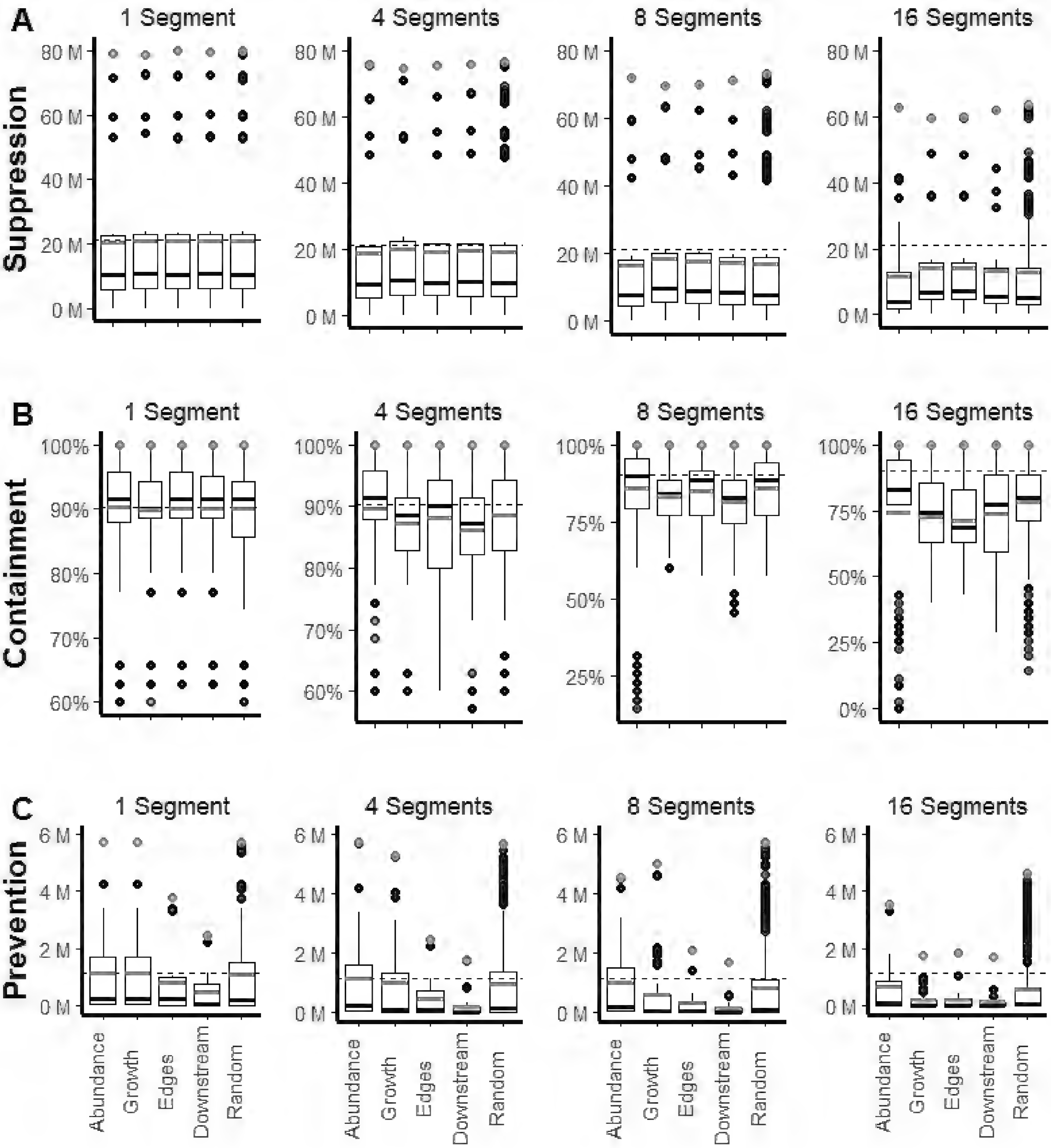

Figure 2. Boxplots displaying the performance of each crayfish removal alternative, except No Removals, across all parameter sets and simulations for each objective **A** suppression: final total crayfish abundance (millions) **B** containment: percent invaded and **C** prevention: total crayfish in the Columbia River (millions). The horizontal black dotted line represents the expected value outcome under No Removals. In each boxplot, the red line is the mean, the black line is the median and the red point is the maximum value. In subfigures **A–C**, the facet plots represent 1, 4, 8 and 16 segments receiving removal effort. We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream and Target Random as Random.

Since all the objectives were based on either final population abundance (suppression), final distribution (containment) or cumulative abundance (prevention), we did not focus on changes in the population over time. However, under all alternatives, the abundance of crayfish slightly increased over time (Suppl. material 1: figs S3, S4).

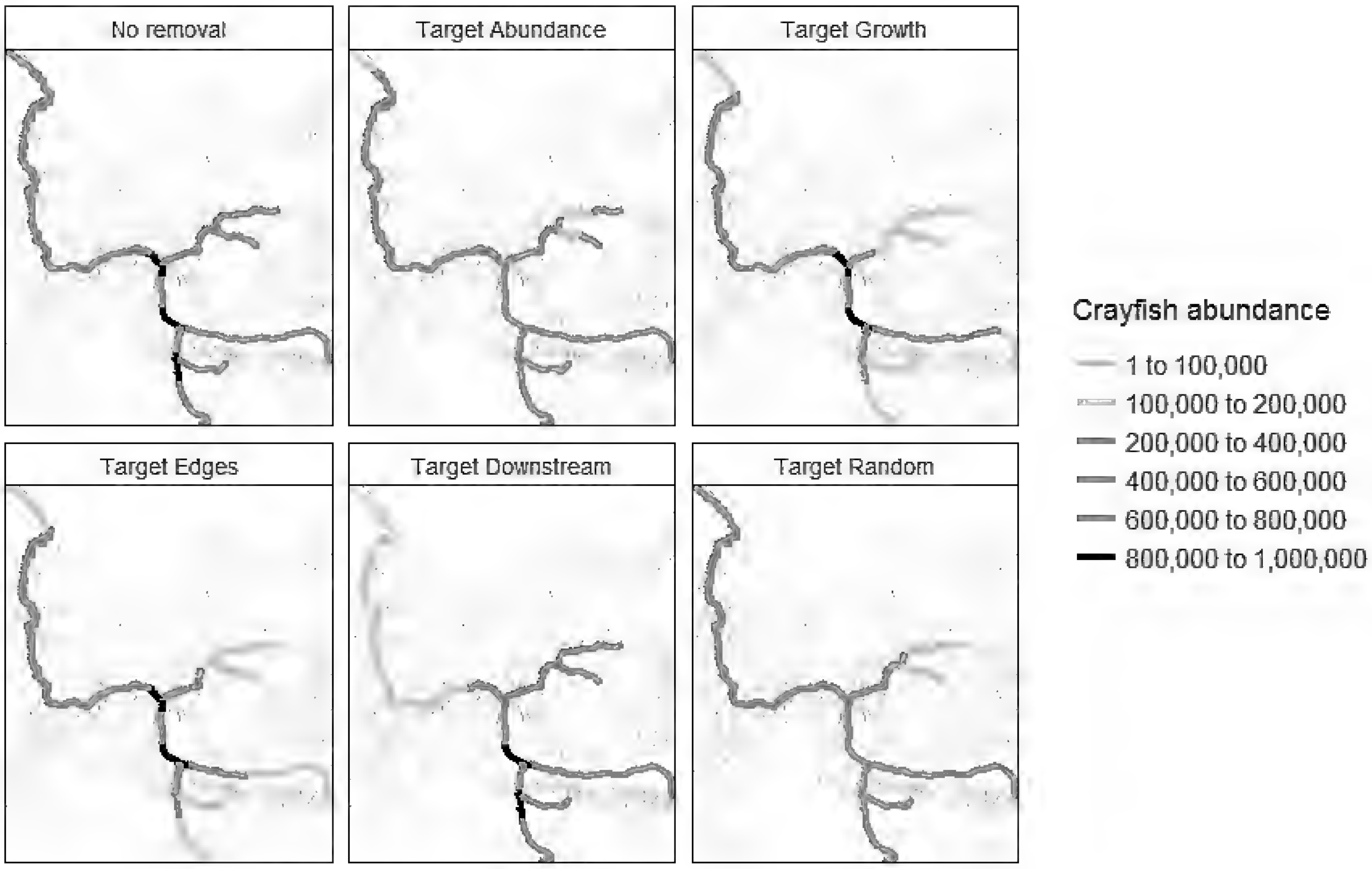

Figure 3. Segment-level total crayfish abundance after 7 years of management, averaged across simulations and parameter sets for each strategy (No removal, Target Abundance, Target Growth, Target Edges, Target Downstream and Target Random) with 16 segments of removal effort. The colours show segment level abundance.

Table 2. Consequence table of simulation results for rusty crayfish (*Faxonius rusticus*) removal in the John Day River, Oregon, USA, based on the expected value decision criterion. The first column indicates the alternative and the second to fourth columns represent the expected value for that alternative under each of three objectives, with M representing millions of crayfish. The bold text within a cell represent the minimum (i.e. preferred) expected value for each objective, for a given number of segments receiving removal effort. The fifth column indicates the alternative, if any, that dominated the alternative in the row, again for a given number of segments receiving removal effort. An alternative is Pareto efficient if no alternative dominates that alternative, indicated with "None". We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream and Target Random as Random.

Alternative management strategy, no. segments of removal effort	Objective (expected value)			Dominated by X Alternative
	Suppression (in millions)	Containment (%)	Prevention (in millions)	
No removals, 0	21.13 M	90.3%	1.15 M	None
Abundance, 1	**20.52 M**	90.2%	1.15 M	None
Growth, 1	20.83 M	**89.7%**	1.15 M	None
Edges, 1	20.68 M	90.0%	0.83 M	None
Downstream, 1	20.81 M	90.1%	**0.48 M**	None
Random, 1	20.61 M	90.0%	1.10 M	None
Abundance, 4	**18.82 M**	89.6%	1.14 M	None
Growth, 4	20.05 M	87.2%	1.01 M	Downstream, 4
Edges, 4	19.24 M	88.1%	0.48 M	None
Downstream, 4	19.37 M	**86.2%**	**0.18 M**	None
Random, 4	19.00 M	88.6%	0.96 M	None
Abundance, 8	**16.67 M**	85.7%	1.02 M	None
Growth, 8	18.34 M	83.1%	0.58 M	Downstream, 8
Edges, 8	17.92 M	85.1%	0.31 M	Downstream, 8
Downstream, 8	17.32 M	**81.4%**	**0.15 M**	None
Random, 8	16.93 M	85.7%	0.83 M	None
Abundance, 16	**11.81 M**	74.1%	0.67 M	None
Growth, 16	14.25 M	72.9%	0.22 M	Edges, 16
Edges, 16	14.24 M	**71.4%**	0.22 M	None
Downstream, 16	13.17 M	73.7%	**0.15 M**	None
Random, 16	12.78 M	78.3%	0.56 M	None

Table 3. Consequence table of simulation results for rusty crayfish (*Faxonius rusticus*) removal in the John Day River, Oregon, USA, based on the mini-max decision criterion. The first column indicates the alternative and the second to fourth columns represent the maximum predicted value for that alternative under each of three objectives, with M representing millions of crayfish. The bold and underlined text within a cell represent the minimum (i.e. preferred) of the maximum values for each objective, for a given number of segments receiving removal effort. The fifth column indicates the alternative, if any, that dominated the alternative in the row, again for a given number of segments receiving removal effort. An alternative is Pareto efficient if no alternative dominates that alternative, indicated with "None". We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream and Target Random as Random.

Alternative management strategy, no. segments of removal effort	Objective (expected value)			Dominated by X Alternative(s)
	Suppression (in millions)	Containment (%)	Prevention (in millions)	
No removals, 0	80.30 M	100%	5.73 M	N/A
Abundance, 1	79.10 M	100%	5.72 M	None
Growth, 1	**78.72 M**	100%	5.73 M	None
Edges, 1	79.80 M	100%	3.78 M	Downstream, 1
Downstream, 1	79.58 M	100%	**2.45 M**	None
Random, 1	79.91 M	100%	5.72 M	Abundance, 1 & Downstream, 1
Abundance, 4	75.77 M	100%	5.72 M	Growth, 4 & Edges, 4
Growth, 4	**74.68 M**	100%	5.31 M	None
Edges, 4	75.52 M	100%	2.45 M	None
Downstream, 4	76.11 M	100%	**1.76 M**	None
Random, 4	76.84 M	100%	5.72 M	All
Abundance, 8	72.32 M	100%	4.53 M	Edges, 8 & Downstream, 8
Growth, 8	**69.91 M**	100%	5.00 M	None
Edges, 8	70.08 M	100%	2.10 M	None
Downstream, 8	71.49 M	100%	**1.70 M**	None
Random, 8	73.30 M	100%	5.72 M	All
Abundance, 16	63.04 M	100%	3.54 M	Growth, 16 & Edges, 16 & Downstream, 16
Growth, 16	**59.64 M**	100%	1.75 M	None
Edges, 16	59.80 M	100%	1.85 M	Growth, 16
Downstream, 16	62.13 M	100%	**1.70 M**	None
Random, 16	63.61 M	100%	4.61 M	All

Discussion

We used a spatially explicit population model to simulate rusty crayfish population growth, movement and removal in the JDR and evaluated different management strategies across various effort levels (i.e. number of locations receiving management). We evaluated the performance of all alternatives in meeting objectives of suppression (i.e. minimise the overall population size or total abundance of rusty crayfish), containment (i.e. minimise the range size or spatial extent of rusty crayfish in the JDR) and prevention (i.e. minimise the number of crayfish entering the Columbia River). Our results point to three major outcomes with respect to comparing spatially explicit management alternatives for an invasive species.

First, all strategies involving removal of invasive crayfish performed better than No Removals on every objective in terms of both decision criteria, yet the optimal strategy often varied by objective, decision criteria or the level of removal effort. For example, if the prevention objective was the priority, the Target Abundance strategy would be preferred for a risk-neutral decision-maker (expected value decision

criterion), but for a risk-averse decision-maker (mini-max criterion), the Target Growth strategy would be preferred (Tables 2, 3, Fig. 2). The optimal strategy for the containment objective in terms of the expected value criterion varied across the number of segments that received management (Table 2). However, Target Downstream was consistently the best strategy for the prevention objective across all numbers of segments receiving management and across the two decision criteria, yet this strategy performed poorly on the suppression objective (Tables 2, 3, Fig. 2). In addition, for this objective, removing at one segment under the Target Downstream strategy performed better than any other strategy with four segments of removal effort (Table 2). The Target Downstream strategy is similar to other efforts in freshwater invasive species management to reduce spread rates into an uninvaded area (Rytwinski et al. 2019). For example, to minimise stone moroko (*Pseudorasbora parva*) spread in England and Wales, resource managers targeted management at lakes that were located on the floodplain (Britton et al. 2011). In addition, a study of invasive signal crayfish (*Pacifastacus leniusculus*) in Europe revealed that removing crayfish at the leading front of the invasion may delay colonisation to new areas (Moorhouse and Macdonald 2011).

Second, because no single management strategy performed the best across every objective and decision criterion, trade-offs amongst objectives are unavoidable. We found that the Target Downstream strategy was the only strategy that was Pareto efficient (i.e. not dominated by another strategy) regardless of the number of segments receiving removal effort and regardless of the decision criterion (Tables 2, 3, Fig. 2). This is because the Target Downstream strategy was always the best strategy for the prevention objective. This result differs from findings in terrestrial invasive species contexts that suggest targeting the core of invasion (e.g. Baker (2017); Lustig et al. (2019)), equivalent to the Target Abundance strategy here, is most effective. However, our result is similar to findings for invasive weed management, in which targeting outlier invasions can be effective (Bossard et al. 2000). In many invasive species management contexts, preventing spread into a new area is an important objective, especially when eradication is not feasible (Green and Grosholz 2021). For example, a primary objective of bigheaded carp (*Hypophthalmichthys spp.*) management in the mid-western United States is to minimise spread into the Great Lakes (MacNamara et al. 2016). In addition, the U.S. Forest Service developed a campaign for invasive spongy moth (*Lymantria dispar*) called "Slow the Spread" to minimise new invasions (Grayson and Johnson 2018). Hence, for a widespread invasion, management strategies that best prevent spread into new areas may be preferred. However, when managers make decisions regarding spatial management, it is important to acknowledge that some strategies may not be mutually exclusive and management locations may overlap (e.g. target growth and target edges strategies may involve removal at the same locations).

Third, as expected, it is better to conduct management at a higher intensity. For example, the expected value outcome of the suppression objective under the Target Abundance strategy showed a 3% improvement comparing No removals to one segment receiving management, an 8% improvement comparing 1–4 segments managed, an 11% improvement comparing 4–8 segments managed and a 29% improvement when comparing 8–16 segments receiving management. In general, the outcomes of the best alternative under all objectives and decision criteria improved with increasing management intensity (Tables 2, 3). A variety of invasive crayfish management studies have also recognised that higher intensity removals

achieve better management results (Hansen et al. 2013; Perales et al. 2021; Reisinger et al. 2024). For example, a whole lake invasive rusty crayfish removal study in Wisconsin, USA, showed that intensive trap efforts could suppress rusty crayfish populations (Hein et al. 2007). However, although intensive crayfish removal may effectively suppress populations, especially in closed systems, these intensive efforts often come at a significant economic cost and are increasingly challenging to conduct in open systems like rivers (Fausch and García-Berthou 2013).

Cost is often a major consideration in management (Epanchin-Niell 2017). To account for this, we considered alternatives with varying intensities (i.e. number of segments with removal effort) as a proxy for cost. Implementing a “proxy” for cost is a simple and effective way to help identify the degree to which management outcomes may improve if budget is increased. Here, we showed that increasing the number of segments that received management greatly improved outcomes in suppressing the population, yet there were only marginal benefits in improving outcomes for the prevention objective (Fig. 2).

We relied on simulations of a population model to conduct this study and, with all such studies, there are some limitations to acknowledge. In terms of the ecology of rusty crayfish, in our model, temperature was the only covariate included, but other environmental factors may be important. For example, river flow results in variability in dispersal rates of crayfish (Ehrlén and Morris 2015), though it would be challenging to simulate at the scale of our study. In addition, we assumed that every location was available for removal, which may not be the case in reality due to restrictions in access and this assumption may impact management outcomes. For instance, Bertolino et al. (2021) showed that restricting access of natural resource managers to private property can cause delays and lead to more costly management. In addition, our model assumed a high level of trap coverage in each segment and various levels of trap coverage could be evaluated in future studies. Finally, the only management technique we considered involved removal of adult crayfish (i.e. older than 1 year old) via physical trapping. Removal techniques involving juvenile crayfish are rare and difficult to implement. Invasive crayfish management programmes will benefit from studies that identify novel, effective techniques (e.g. biocides, Manfrin et al. (2019)).

We selected segments for management, based on perfect knowledge of the system, which will not be the case in real applications. If we do not have perfect knowledge of the state of the system, we would need to rely on monitoring data to identify removal segments, allowing for the implementation of dynamic or adaptive management (Lyons et al. 2008; Williams and Brown 2014). We attempted to create this case study in an adaptive management context, which relied on creating a Bayesian estimation model for abundance. However, we were unable to produce reasonably accurate estimates, likely because we were collecting data from only a subset of segments in only four months of the year. If management were to occur more frequently or additional data streams were integrated (e.g. detection-non/detection or radio telemetry data), an adaptive management framework may be appropriate, as abundance and other parameters could be better estimated. However, our results provide insight into the management strategies that may be most effective, as well as their overall effectiveness in the best-case scenario, when knowledge about the system is perfect.

The JDR represents a particularly challenging system, in terms of the extent of the basin and of the crayfish invasion, making it difficult to accurately manage or

monitor the entire basin. While managers are not currently removing crayfish in the JDR, we provide context on the potential effects of management which could be used by future decision-makers. Although we showed that removing crayfish resulted in better management outcomes than No Removals, on average, no strategies resulted in eradication, successful containment or prevention of crayfish moving downstream into the Columbia River. Therefore, rusty crayfish invasion in the JDR can serve as a precautionary tale, as management outcomes would have likely improved if management had begun earlier in the invasion process (Messager and Olden 2018). Therefore, we emphasise the value of early detection and rapid response for minimising the impacts of invasive species before the invasion becomes too large for management to be effective (Reaser et al. 2020).

In conclusion, we provided an approach to simulate an aquatic invasive species in a complex riverine environment. In general, there are very few applications of population models that evaluate spatially explicit management in riverine contexts (Corrales et al. 2020). We described a flexible modelling framework that integrated different spatial management strategies and is broadly applicable to different species and regions of interest. Spatially explicit population models can offer natural resource managers a cost effective tool to examine management alternatives.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: BKT, JDO, SJC. Data curation: JDO. Formal analysis: BKT. Funding acquisition: JDO, SJC. Investigation: SJC, JDO, BKT. Methodology: SJC, BKT, JDO. Supervision: SJC, JDO. Validation: JDO, SJC. Visualization: JDO, SJC, BKT. Writing - original draft: BKT. Writing - review and editing: JDO, SJC, BKT.

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Data availability

R scripts and data sources underpinning the analysis of this paper are deposited on GitHub at: https://github.com/Quantitative-Conservation-Lab/Thompson_etal_2024_NeoBiota.

All result files can be found at: https://doi.org/10.5281/zenodo.12761044. References to parameter values used in the model and supplemental figures can be found in Suppl. material 1.

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Supplementary material 1

Additional details of the crayfish model and supplemental figures

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